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## THE MEANING OF TREE-LIFE.

BY HENRY L. CLARKE.<sup>1</sup>

Few there are, even among thoughtful botanists, who seem to clearly realize how broad a lesson on the life-history of plants is written in the trees that make the great forest regions of the world. Whether we stand among the palms of the tropics, or the pines of the north, or the congeners of the poplar and oak, we feel instinctively that there is an impressive depth of meaning in the very aspect of a tree. And it is no deception of the fancy. Tree-life represents the culmination in the work of one of the two great factors, reproductive energy and vegetative energy, that together shape the course of plant-development. The history of plants records a constant two-fold struggle; on the one hand the effort of plant-life as a whole to perpetuate itself by improving its methods of reproduction; on the other, the stand for self-preservation made by each distinct individual or species or group,—a stand that can be taken only through sheer force of vegetative luxuriance. But these two phases of the struggle for existence have by no means been independent of each other; they have acted together in varying ratio in the making of every type, though their respective influences have culminated in widely separated forms. As the highest outcome of evolutionary progress in the character of floral organs we point to

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the orchids, among Monocotyls, and the kinsmen of the golden-rods and asters, among Dicotyls; as the monarchs of vegetative energy stand the tree-ferns and towering palms of the tropics, the Red-Woods of California, the Eucalyptus of Australia, and our forests of mighty oak. Thus the classification systems of modern botany that review in the clearest scientific light the evolutionary relationships of species, genera, orders, and classes, present to us only one side of the problem of plant-life; the dynamics of vegetation is the other. We may know that the Coniferae are among the most primitive of flowering plants, and the Orchidaceæ and Compositæ among the highest; but why do we find our orchids and composites growing as stunted herbs in the very shadow of conifers that are giant trees? Which is master of the situation? Systematic botany has not fulfilled its mission until it has grasped both sides of the two-fold relation that the contrasting types bear to one another.

Far back in geologic time the dawn of tree-life came almost with the beginnings of vegetation. What the earliest of those beginnings were we can scarcely even conjecture, but going back as far as fossil botany will carry us with certainty, we may conceive something of the conditions under which the primitive plant-world was fostered. Consider the probable conditions of the Cambrian and Silurian Ages. However, scant the records that we hold, they are yet sufficient to give us some suggestions of inestimable importance. Past question the earliest forms of plant-life were denizens of the water, developed in the seas and lakes of Pre-Cambrian times. From their aquatic habitats they must have first gradually emerged, as the cooling of the primordial continents permitted, and the strengthening of their own anatomical characters favored, into the swamps and marshes, and then step by step mounted the higher regions of the dry land. The oldest fossil types we with certainty know of were far from the beginning of the scale; they could only have been products of ages of development that must forever remain to us almost a total blank. The world of Silurian times was probably a torrid zone from pole to pole, a condition traceable in large part to the insular

character of its continents. The surcharging of the atmosphere with water-vapor meant excessive precipitation, and the shallow-water conditions obtaining around the continental islands, together with the probable lowness of these isolated landmasses favored the existence of extensive swamps and marshy flats, in which the water may have been either fresh or brackish. Here in these primordial swamps the vegetation destined to cover the earth made its determined struggle for existence. On the higher land there was too much heat; in the seas there was too much water; in the swamps was the requisite combination of water, heat, and heavy carbon-laden air. Under such conditions the first types that took possession must have spread and multiplied with incredible rapidity. What followed? Inevitably the primitive low-growing plants crowded closer and closer together and became a rank tangle of growth; where there had been at first plenty of room for every individual to spread, there were now many struggling for the mastery of each square foot of swamp. All had a foot-hold in the earth but only the few that stood the highest could drink in the feeble rays of the cloud-bedimmed Silurian sunshine. Then the real battle for the light began in earnest, the stronger against the weaker, the older established types against the newer ones whose foot-hold was less certain; higher and higher the rank swamp-growth rose, all its members struggling together for the light and open air. And so in the wierd gigantic club-mosses of those far-off times we see the prophetic beginnings of the tree-life of to-day; and to trace the development of the majestic forests of the present from those dank swampy jungles of the past is the problem before us. It would seem at first glance that in the primæval jungle "might made right," if ever it made it anywhere. But no! the "survival of the fittest" worked in two directions. Vegetative luxuriance was a tremendous factor in determining the survival of types, vastly more so then than now; but wherever an improvement in the character of reproductive organs increased the certainty with which any plant could perpetuate its race, that gain could often far outweigh the superior vegetative luxuriance of all competitors. This second factor in the "survival of the fittest"

has been steadily waxing in importance from primæval times, while the other has begun to wane. In the midst of the Silurian jungle, where the energy of plant-life was strained to the utmost limit of activity, new forms originated. What was their fate? They could not overpower the strongly established older forms crowding all about them, so either they must perish or push outward toward the open margin, where there was room to fight. Thus the swamp-margin became the tension-line between the uninhabitable higher land and the old strong hold of the jungle, and on this tension-line stood the vanguard of the world's future vegetation. On its outer edge the tension-flora faced a new and untried habitat, and then, as now, a highly specialized habitat meant highly specialized inhabitants. The untried ground could not be conquered by sheer force of vegetative luxuriance, for by their very nature the new conditions were physically opposed to the established order of things in plant-life. The all-powerful factor in accomplishing the conquest was increased capacity for variation and the adaptive evolution of old structural types into higher stages of organization. Clearly, this tendency predominated and pervaded the whole tension-line flora, but its maximum was toward the outer edge. So here were ranked the low-growing herbaceous forerunners of coming ages,—forms that were humble in their growth, because of the physical obstacles opposing them; and highly specialized, because their structure did not possess the obstinate stability of the patriarchal tree-life behind them. For the same reasons the character of the undergrowth in the jungle must have always been ages in advance of the arboreal monarchs towering overhead. But on the inner side of the tension-line, vegetative luxuriance was not only possible and potent but also obviously a necessity, for there could be no abrupt demarkation between the marginal and central regions. Here, then, where the jungle-flora merged into the tension-flora, was the stronghold of the rising generations, the newer higher types, of tree-life. Here, in early Silurian times, must have stood the ancestral types of the great tree-ferns and calamites and conifers that were to be supreme in the Carboniferous and early Mesozoic.

The history of plant-life through the later Silurian and the Devonian Age records the first strong establishment of a truly dry-land flora, a substantial foreshadowing of the Mesozoic. The changes in physical conditions of course furthered this result no less truly than did the adaptive evolution of organic forms. In the dry-land forests of the Devonian rose the vegetation whose future developments should hold dominion when the primordial swamps had disappeared from the earth. But these terrestrial forests evidently had the effect of removing an immense part of the pressure upon the old swamp-jungles by becoming the main refuge and stronghold of the new types crowded out at the old tension-line. This, together with the physical changes recorded in the rock-systems of the times, gave full vent to the gathering vegetative energy that reached such a stupendous culmination in the mammoth swamp-flora of the Coal Age. Here was a turning point in plant-history. With the dawn of the Mesozoic came the clear prophecy of modern conditions. The dry-land forests of the Reptilian Age were the full realization of the conditions foreshadowed in the Devonian. Out of the swamp-forests of the Carboniferous came some of the highest Lycopods, great Tree-Ferns, and giant Equisetums. Down from the Devonian came the Conifers of the yew-family; and as reminders of the old genus *Cordaite*s the new order *Cycadaceæ* appeared. Undoubtedly it is impossible to believe that the swamp-flora of the coal seams represents anything like the whole flora of the Carboniferous Age. There must of necessity have also existed then a great transitional dry-land flora between the terrestrial forests of the preceeding Devonian and the succeeding Jura-Trias. Much of the strata called Devonian or Mesozoic probably represents this transition and was synchronous in its formation with the accumulation of the coal. Part of the transition is clearly observable in the noncarboniferous formations included between the coal-seams. While the preparations, begun in the Devonian, for the great Mesozoic forests were slowly and surely progressing, the old vegetation of the swamp-jungle swept up to its culmination, and marked by its decline the close of the Paleozoic Era. The early Mesozoic

became the age of Gymnosperms. Vegetation had come upon a new battle-field, the terrestrial forest-ground, and only the most highly organized types of preceeding ages were fitted to enter the struggle. Many of the Tree-Ferns and Equisetums were still powerful, but the supreme dominion passed over to the Conifers and their allies, the Cycads. The great forests of Conifers had their undergrowth and their tension-lines, and here the development of new types was progressing with probably even greater activity than in the tension-floras of earlier times. The greater complexity of the conditions confronting a terrestrial flora over those confronting a swamp flora would necessarily mean more elaborate specialization. While the ancient coniferous tree-forms were mounting to the fulness of their power the first types of the higher flowering-plants were beginning to appear; and with the opening of the later Mesozoic, the Cretaceous, two new groups of tree-life came upon the stage as worthy competitors of the old established Gymnosperms. One was the order Palmaceæ, representing the Monocotyledonous Angiosperms; the other was the amentaceous hardwood tree-families, representing the Dicotyledons. The opening chapter in the history of these two groups is a matter of peculiar interest.

It is probable that the two groups were almost, if not quite, synchronous in their rise; though there is some reason to believe that the Palmaceæ, or at least their forerunners, the Pandanaceæ, are slightly the older. As has been indicated the central strength of the Mesozoic forests was undoubtedly held by the coniferous trees; and probably by far the greatest strength was vested in the near allies of the Cypressess, Pines, and Firs,—representing the tribes Cupressineæ, Taxodiæ, Abietineæ, and possibly also Araucarieæ,—while the older sub-order Taxineæ, the broad-leaved Conifers of the Yew family, were rather crowded out toward the tension-line margins along with the Cycads and Tree-Ferns. Among these last the first low-growing Tree-Palms probably rose, as the products of a long course of elaborate specialization. It is more than possible that the Pandanaceæ represent at least in part a transitional stage between some of the higher Gymnosperms and the

Palmaceæ; and it is well worthy of note that the aerial roots of the Screw-Pines, the Pandanaceæ, are a living memorial to the position they originally held on the shore-margin of a forest tension-line. The habit of growth of the Palmaceæ most strikingly suggests that their first competitors were Tree-Ferns and Cycads, even as they are in many regions to-day. It seems as if the first Palms had met the Mesozoic Tree-Ferns and Cycads on their own ground,—the forest margin,—with their own weapons—the tall aspiring trunk topped with a crown of leaves. And by their general higher character of organization the Palms ultimately asserted their preeminent superiority. The wide contrast between the floral characters of the Palmaceæ and those of the Gymnosperms presents a difficult problem. There is a strong likelihood, however, that the spadiceous inflorescence of the Screw-Pines and Palms is a highly specialized development from the cones of some aberrant Cycad or Conifer. At least all the probabilities indicate that the spadiceous Monocotyls approach much nearer the Gymnosperms than do any of the non-spadiceous ones. All this has evidently a most significant bearing on the question before us, of the Palms' place in Nature. We have seen that the vegetative character of the Palms was widely different from that of the dominant Conifers; and now we note that their floral organs were also widely different, and in fact far more decidedly unlike the cones of the Cypresses and Pines than are the "catkins" of the hardwood dicotyl trees.

There are a half-dozen or more tree-orders among the Dicotyls that should really stand apart as forming a small subclass quite decidedly distinct from the rest of the Dicotyls. As the principal orders of this group may be named the Juglandaceæ, Myricaceæ, Salicaceæ, Betulaceæ, Fagaceæ, Ulmaceæ, Platanaceæ, and a couple of others. These have been called the Amentaceæ, or the Diclinæ, and might be regarded as a subclass. Except in the approach of Ulmaceæ to the Urticaceæ, the Diclinæ stand clearly apart as a distinctive highly specialized alliance of trees and shrubs. Their relation to the Mesozoic Gymnosperms is an interesting question. In general habit of growth and in the character of their wood they evidently make a close approach to the Conferæ.



The amentaceous inflorescence predominating in the group bears a decided likeness to the cones of the Pines and Cypresses. Obviously then, the Diclinæ were the trees best fitted to battle with the central stronghold of the Mesozoic coniferous forest, and probably they were first fully developed on the inner portion of the tension-line, face to face with the strongest of the Conifers. Behind them, toward the outer edge stood the Tree-Ferns, Cycads, and Palms; but which, we may ask, were the Conifers that stood closest round about, among and before them? Probably the sub-order Taxineæ, the fraternity of broad-leaved Taxites and Ginkgos. The power of this most ancient group of Conifers had, as we have seen, waned, and they must have been driven toward the outskirts of the forest by the stronger Cupressineæ and Abietineæ. Here they must have met the early Diclinæ. Where did the Diclinæ develop the broad flattened leaf-blades that so strikingly distinguish their foliage from that of our living Coniferæ? Where, if not in a competitive struggle with the broad-leaved Taxineæ of the Mesozoic forest-margin? The ancient Taxineæ had reproduced in their foliage something of the character of the fern-fronds; the newer Pinaceæ had rather imitated and exaggerated the scale-leaves of the great Carboniferous Lycopods. And finally, the broad leaves of the Taxineæ were perpetuated, under greatly improved and elaborated forms, in the Diclinæ. Through the Cretaceous the Coniferæ rose to the zenith of their power; the Tree-Ferns and Cycads weakened; the Palmaceæ and Diclinæ, more particularly the latter, fast gathered strength toward the dominion they claimed in the succeeding Tertiary. Meantime, in the undergrowth and on the open margins of the forests, and on the open country that did not support a growth of trees, the evolution of the higher types of Monocotyls and Dicotyls was rapidly progressing. Many of the stronger forms became shrubs, and here and there a peculiarly favored type rose from lowly herbaceous to arborescent habit, and thus founded a new tree-group. Such, for instance, were the Magnolias and Tulip-Trees and Maples and many others. In all this we read an increasing complexity in the conditions presented to onward struggling plant-life, and here a vitally important point rises for our consideration.

*(To be continued.)*